The Journal of HEREDITY

BIRTH OF A CELL

John Belling—Cytologist

Gene-Interaction in the Fowl

A "Buffalo" Calf

Races of Man

Inheritance of Multiple Sclerosis

Fish Genetics

"Tempo-Genes" in Man

A Second "Liguleless" Gene in Maize

VOLUME 24 AUGUST, 1933 NUMBER 8

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An incorporated organization devoted to promoting a knowledge of the laws of heredity and their application to the improvement of plants, animals, and human racial stocks

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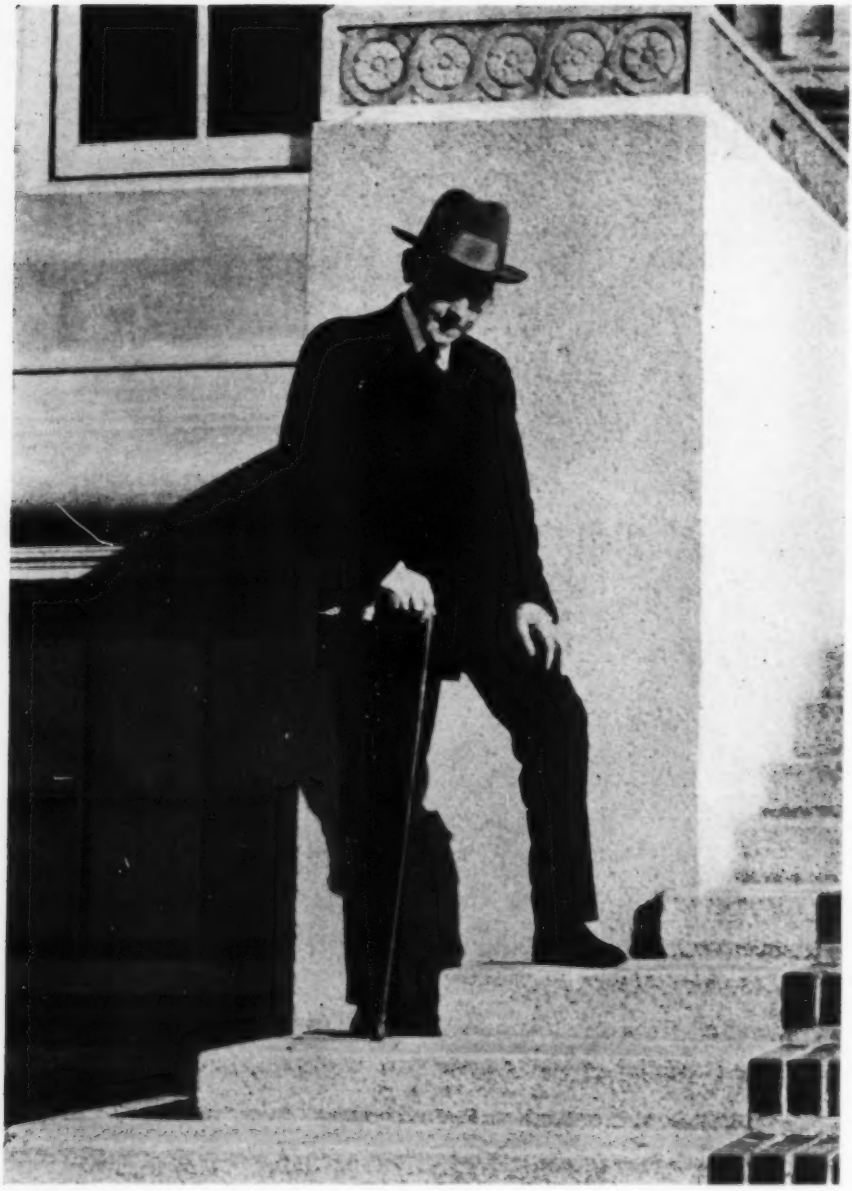


DR. JOHN BELLING

1866-1933

Science progresses by improvements in technique and by the formulation and experimental verification of fruitful hypotheses. Dr. Belling in the years he spent studying the microscopic structure of the living cell made fundamental contributions both to the technique of cell exploration and to the interpretation of the phenomena he observed. His death removed one who had made great contributions to our knowledge of those fundamental units of life—the chromosomes.

JOHN BELLING

Pioneer in the Study of Cell Mechanics

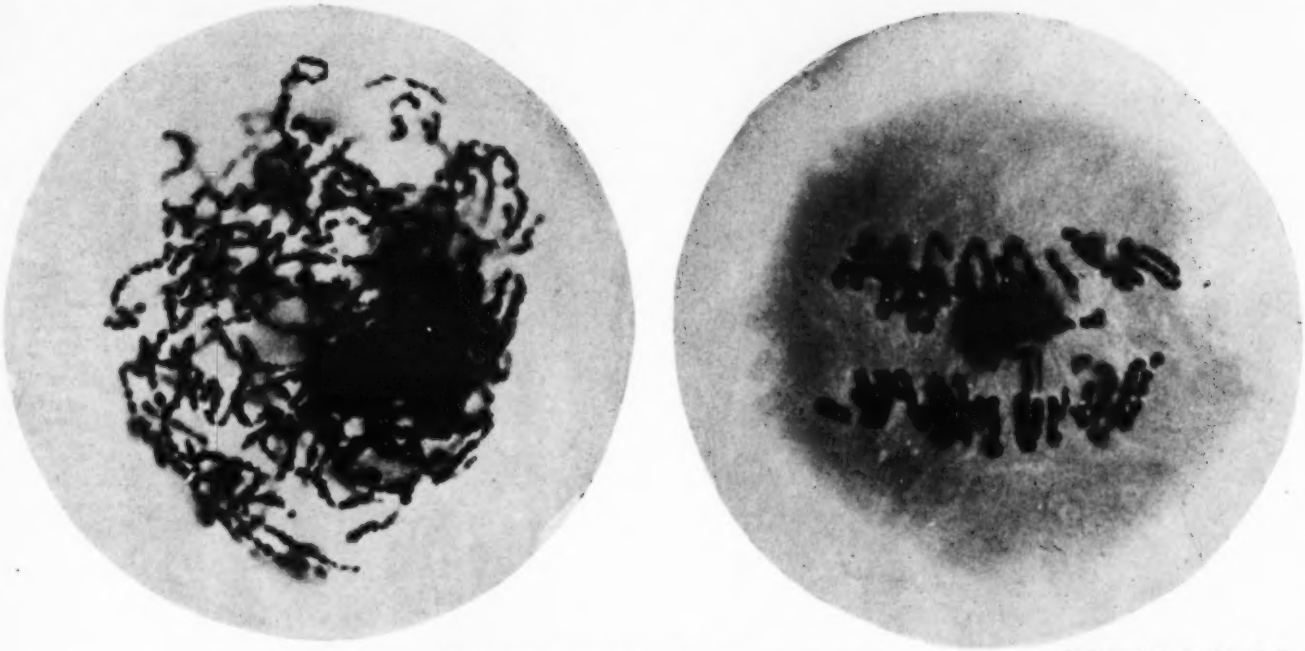
DR. JOHN BELLING, Cytologist in the Carnegie Institution of Washington and Research Associate in Genetics in the University of California, died of heart disease in Berkeley, California, on February 28, 1933. Though frail physically, even in his later years he was the envy and admiration of his closest associates because of the versatility of his keen and active mind and his ceaseless devotion to research and kindred pursuits.

Born in Aldershot, England, in 1866, Dr. Belling was educated in private and public schools, spending two years at the University of Birmingham and receiving the degree of B. Sc. at the University of London in 1894. After teaching in the lower schools, he was research lecturer in the Horticultural College at Swanley, 1895-98, and for the succeeding three years, teacher of science at Wells, England, and Llandidloes, Wales. He received the honorary degree of Sc. D. at the University of Maine in 1922.

In 1901 he went to the Island of Christopher in the West Indian service of the Imperial Department of Agriculture and remained in that service until 1907 when he went to Florida and joined the staff of the State Agricultural Experiment Station where he worked one year as Assistant Horticulturist and eight years as Assistant Botanist. Using the same systematic methods which characterized his later scientific career, be began by collating, abstracting and indexing sources of information on the guava, mango, papaya and hundreds of other tropical and subtropical economic plants. He prepared an index of previous publications of the Experiment Station and the Florida State Horticultural Society and became editor of all the publications of the Station. His first outstanding scientific contribution was a treatise on the cytology of polyembryony in the mango, *Mangifera Indica* (*Florida Agr. Exp. Sta. Report*, 1908, pp. cx-cxxv, pls. vii-x). During this first year in Florida he also published numerous press bulletins and articles, among them one titled "Beautifying Florida Towns," which indicates the deep appreciation of the beauties of nature that characterized his whole life and endeared him to the few who came to know him intimately.

In 1910 Dr. Belling undertook an investigation of the genetics of certain interspecific hybrids in the genus *Mucuna* (*Stizolobium*) which led to several discoveries of fundamental importance in genetics and resulted in the publication of seven valuable contributions of which the last two were: "The mode of inheritance of semi-sterility in certain hybrid plants" (*Zeit. ind. Abst. Vererb.* 12:303-342, 1914) and "Inheritance of length of pod in certain crosses." (*Jour. Agr. Res.* 5:405-420, 1915).

After a period of several years, during which he was not officially connected with any institution, Dr. Belling was appointed Cytologist in the Station for Experimental Evolution of the Carnegie Institution of Washington at Cold Spring Harbor, Long Island, in 1921. There he worked with Dr. A. F. Blakeslee on the cytology and genetics of *Datura stramonium*, a line of research which led to discoveries of outstanding importance in biology. Through brilliant cyto-genetical analysis Belling proposed his hypothesis of segmental interchange, now generally known as reciprocal translocation, between non-homologous chromosomes. This hypothesis was the key to the solution of some of the most puzzling problems in modern genetics. Successful analysis of the nature of the secondary trisomic mutants in *Datura* depended primarily on this hypothesis. Later the same principle facilitated the analysis of other difficult problems in the cyto-genetics of *Oenothera*, *Pisum* and *Zea mays*. The original announcement of this im-

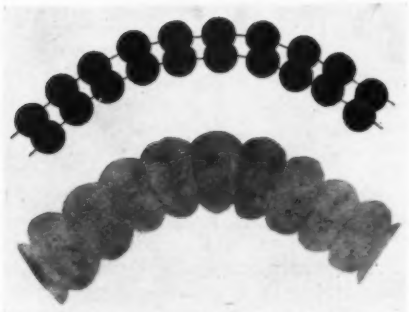


Photographs by Dr. John Belling

CHROMOSOMES OF THE LEOPARD LILY

Figure 1

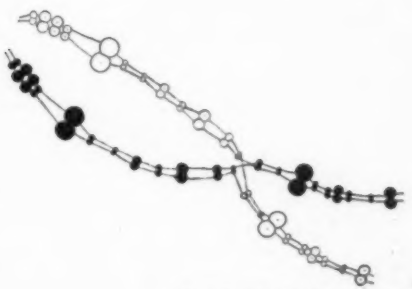
These two photographs were made by Dr. Belling during the intensive search for the gene which he undertook after he went to California in 1927. Since the chromomeres of the Leopard lily are better defined than in many other plants, this species constitutes ideal material for such studies. In the stage of development shown in the photograph at the left Dr. Belling counted over 2,200 of the "chromomere beads" which he believes to contain the actual genes themselves. The photograph at the right shows the chromosomes in a later stage of development when they are more compact. The twelve pairs have divided by splitting longitudinally and the "daughter chromosomes" are separating preliminary to the formation of a new cell. Regarding these gene-beads Dr. Belling remarked: "A minute cell sphere with its 2,200 gene pairs suggests the celestial sphere visible to the unaided eye and containing fewer than 3,000 stars which can be seen at one time. These stars were supposed by some to exert a mystic influence on human beings. In the spherical cells of the organism, however, the genes actually do exert specific influences on the life of the organism in question, whether of the lily or of the man. In fact these influences are so great that if the effects of all the thousands of genes in a given organism were added together nearly the whole of its inheritance would be accounted for." Photographs and drawings courtesy of the Carnegie Institution of Washington.



"GESE-BEADS" AND THE GENES THEMSELVES

Figure 2

These drawings show (above) the double string of chromomeres as seen in an onion species after staining. Below is shown a specimen of a similar double string after destaining and squeezing the specimen flat between slide and cover glass. In the center of each chromomere can be seen a minute black dot. These Dr. Belling believed to be the actual genes.



Drawings by Dr. John Belling

HOW GENE STRINGS "CHANGE PARTNERS"

Figure 3

Diagram, from a camera lucida drawing by Dr. Belling, of a tremendously magnified section of the double chromomere-strings in Fritillaria. The fine details of such an exchange between the two chromosomes of a pair can be observed only by such great refinements of technique that cytologists are still not agreed as to exactly what happens.

portant hypothesis was made in 1926 (*Proc. Nat. Acad. Sci.* 12:7-11). This was only one of a series of papers by Belling and Blakeslee, and by Belling alone, on the cytology of *Datura* and certain other flowering plants (*cf. Jour. Genetics* 18:177-205, 1927).

As he had suffered from ill health for several years, in 1927 it was arranged that Dr. Belling should go to California. At that time the Division of Plant Biology of the Carnegie Institution of Washington at Stanford University had not been established; so accommodations were found in one of the laboratories of the Division of Genetics of the University of California in Berkeley. Soon thereafter Belling was provided with a private laboratory which he used for the remainder of his life. During the time that he lived in Berkeley he was annually appointed Research Associate in Genetics in the University without salary, his salary and incidental expenses as Cytologist being continued by the Carnegie Institution.

After coming to Berkeley, Belling entered his period of most productive research and prolific writing. Many different projects were planned and a surprising number were brought to completion within a comparatively short time. Belling's first major undertaking was the study of the finer structure of the chromosomes. An earlier interest in this subject was indicated by a paper published in 1926 (*Brit. Jour. Exp. Biol.* 3:145-147) which reported early experiments with a special technique. He now applied all his energy and skill to this difficult work and was rewarded by discoveries of the first importance. It is impossible to deal adequately with these results in a very few words. Let it suffice, however, to say that he determined by direct observation the number of chromomeres (the globose granules of which chromosomes are composed) in the cells of a lily and showed that this number, about 2,200, agrees with expectations from genetical evidence, since the orientation and behavior of the chromomeres during cell division are such as would be expected if the chromomeres contain the genes. Then, by a special technique, he demonstrated the existence of an ultra-micro-

scopic particle near the center of each chromomere, which he believed actually could be identified with the gene. These "chromomere cores (or genes)" were described and illustrated in a technical paper, "Chromomeres of liliaceous plants" (*Univ. Calif. Publ. Bot.* 16: 153-170, fig. 8, 1931) and in two popular papers (*Carnegie Inst. Wash. News Service Bull.* 2:207, 1932; *Sci. Educ.* 16:369, 1932). (See Figure 2.)

During the last three years Dr. Belling had concentrated his research with unabated enthusiasm and increasing clarity of penetration on a problem of great importance to genetics, viz., the nature of the mechanism of crossing over or interchange of segments between homologous chromosomes. Just two days before his death he had brought to completion the manuscript of his final paper in the series of valuable contributions on this complex problem. This paper (*Genetics*, 18:388-413, 1933) is a masterly presentation of the evidence and application of his hypothesis to cogent genetic data. In order to convey more clearly to others his conception of the mechanism of crossing over and other chromosomal rearrangements, he prepared a series of models which were exhibited by the Carnegie Institution in Washington and New Orleans in 1931-32 and some of these models were shown at the Sixth International Congress of Genetics in 1932. (See Figure 3.)

Cytological Technique

Even a brief review of his scientific career should not fail to mention his many contributions to cytological technique of which the most important is the development of the smear method of preparing pollen mother cells and other tissues, by means of which almost instantaneous killing and fixing of the cell contents are obtained. Various refinements in these methods made possible most of his remarkable discoveries.

In 1930 Dr. Belling published a book, *The Use of the Microscope*, which was very favorably received and has been translated into several other languages. He left an annotated copy which may serve as the basis for a revised edition. Belling also had under way the preparation of a book on "The Study of the Chromosomes," the finished portion consisting of an introduction, three chapters and an extensive glossary. The Carnegie Institution has under consideration the problem of how best to conserve this material.

Rather late in life Belling married Dr. Hannah Sewall, a woman of culture and refinement whose interests had been mainly in the field of social service. The brief span, some five or six years, before her death seems to have been a period of great uplift for him. They enjoyed together the delights of nature study and her influence over his life seems to have been very helpful. There were no children. Belling is survived by a sister, Miss Annie Belling of London, and by a brother, James Belling, of Bishop's Cleeve, near Cheltenham, England.

Though preëminently a scientist, John Belling was by nature a poet. His poems which have been collected and published are truly original and artistic. The "Elegy" is a poignantly beautiful description of outdoor scenes enjoyed with his wife. In an earlier collection, entitled "English Memories," is found the following:

> Gone are the wintry chill and gloom;
> With primrose out, the windflower frail,
> We enter heaven in Bickleigh Vale,
> Now Spring has 'witched the hills to bloom.

Belling's latchstring was always out to earnest inquirers. "Would you like to see the genes?" was a familiar greeting to those who brought him visitors. For students, especially, he always had a cordial welcome and a sympathetic hearing. Nothing was ever too much trouble in imparting knowledge. Impatient of sham or conjecture, he was meticulous in the care which he took with his own writing and he set a standard of excellence in exposition and composition which may well serve as a model for future generations.

University of California, Berkeley. E. B. Babcock.

THE REACTION OF DOMINANT WHITE WITH YELLOW AND BLACK IN THE FOWL

C. H. DANFORTH
Department of Anatomy, Stanford University

SEVERAL lines of experimentation during the past few years have greatly increased our understanding of the inheritance and the interactions of genes controlling colors and patterns in the fowl. One of these concerns the relation between yellow and dominant white, which in itself opens up a larger field for study of genic interaction and physiological thresholds. Some of the genetic relations between black and yellow have been discussed by Dunn[5], the writer[2], and others; while important contributions to black and white, and yellow and white have been made by such students as Davenport[4] Dunn[6], Warren[11] and Serebrovsky[11]. No attempt will be made to review the literature at this time.

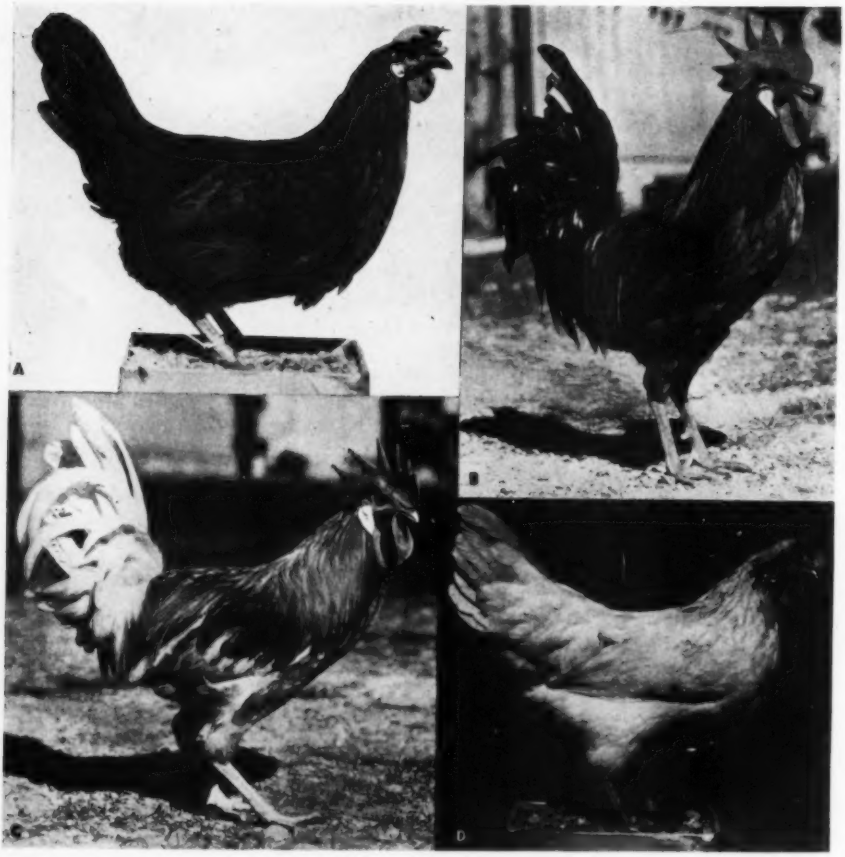
While the data for this paper have come from a number of different experiments, it was the unexpected result of a Buff Leghorn × Black Minorca cross that served to focus attention particularly on this question. The cross was made in continuation of studies on the interrelation of buff and black, the desire being to bring together two strains neither of which carried any pronounced pattern factor. To this end three Buff Leghorn hens, purchased from a well known breeder in the middle west, were mated to a Black Minorca male. Contrary to expectation the chicks which they produced were of two distinct types: black, with brown eye-rings and a yellowish wash anteriorly (the expected type), and white with black legs and a faint sooty cast anteriorly.

The former type developed into males which, when mature (Fig. 4*B*), were reddish yellow with dark under color and black tails, and females (Fig. 4*A*) which were black with some yellow lacing or wash, especially on the neck and breast. When mature the others were males which were yellow, with light under-color and white tails (Fig. 4*C*), and females (Fig. 4*D*) which were white, or slightly sooty, and with a limited amount of yellow distributed very much as in their dark sisters. All F_1 individuals were true to one or the other of these types, indicating a segregation of alternative characters.

The dark F_1 specimens bred *inter se* produced many chicks more or less like themselves, together with some blacks and a few yellows. The light F_1 birds gave, in addition to white chicks, the same three classes as the other group. A light F_1 male mated to pure bred White Leghorns gave 25 pure white offspring and 23 that were white with dark spots or a dark wash. This showed that the light color in the F_1 was a dominant white, and that this white was either the same as, or equivalent to, the ordinary dominant white of Leghorns. In view of the sooty wash of the F_1 and some of the F_2 birds, it might perhaps be suspected that the gene for white was the *B* of Lippincott[10] or the *Tode* of Serebrovsky[11], but no blues of the Andalusian type were produced, and the genetic behavior was not what would have been expected on this supposition. The slight trace of gray was probably due rather to a still different gene for graying which is often met in the Black Minorca genotype and in that of some other dark strains.

Yellow Epistatic to Dominant White

The origin of this suddenly appearing dominant white now became a matter



LEGHORN-MINORCA HYBRIDS

Figure 4

A—A dark F_1 Female, black with yellow in hackle, breast, and, to a less degree, other parts of the plumage; *B*—A male of similar genotype, reddish yellow with dark undercolor and black tail; *C*—A light F_1 male, reddish yellow with light undercolor and white tail (except for black flecks; *D*—A female of similar genotype, white with some yellow in hackle and breast.

An analysis of later generations showed that the light colored birds carried a "dominant white" gene, which almost completely inhibited the development of black, but which had little effect on yellow pigmentation.

of interest. Consequently the three original Buff Leghorn females were tested further. With another Black Minorca male and with a Jersey Black Giant they gave the same two classes of young as before. They were next mated to a Buff Leghorn of a different strain, from which mating only typical Buff Leghorn offspring were obtained. Sixteen eggs from hen *X* gave fifteen clear buff chicks without markings of any kind. From hen *Y* eighteen eggs gave eleven pure buff chicks and six which

were buff with a small dark brown spot on the head. Hen *Z* laid no fertile eggs. Mated to a Jersey Black Giant immediately after this test, *X* produced five white chicks from five eggs, and *Y* four white and three dark chicks from nine eggs. It is clear from these several tests that hens *X* and *Y* carried genes whose tendency toward elimination of color is completely suppressed in individuals homozygous for yellow, but only partly suppressed in those which are merely heterozygous for it. Further, the F_1 tests indicate that the gene in question is probably the ordinary one for dominant white.

This inference is rendered still more likely by the statement of the original breeder that eight years before a White Leghorn male had in fact gained access for a short time to a pen of his Buff Leghorns, although the effects, troublesome for a year or two, were thought to have been long since "bred out"—an interesting example of the practical breeder's methods, and their possible results. Perhaps this "breeding out" may have involved unconscious selection of accessory factors which helped still further to suppress the white.

Relation of Dominant White to Black and Yellow

In view of the circumstances a closer comparison of the F_1 dark and light types became of interest. The surface color of both kinds of males is much the same, except as it is influenced by the respective undercolors, dark in one type, light in the other. The tails present the most striking contrast and give a clew to the real difference between the two forms. This difference seems to be limited almost exclusively to the black and white, the yellow being only slightly involved. A similar relation obtains in the females. In other words, the gene for dominant white is capable of almost completely suppressing black pigmentation, while producing only a limited effect on the yellow.

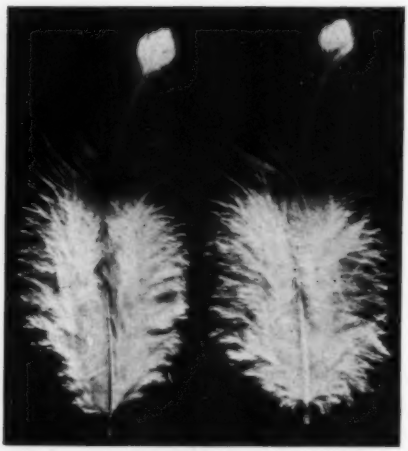
If a dark F_1 individual of either sex were to have all its black pigment dissolved from the feathers and only a little of the yellow removed, it would become a typical representative of the light type. This explains the result of breeding experiments so far as they have gone and is consistent with the findings in a number of other tests involving the standard dominant white gene.

It may be of passing interest to recall in this connection that among wild birds "partial albinos" (whose genetic constitution is generally unknown) often show what seems to be a similar differential in the resistance of yellow and black to white. For example, robins are sometimes nearly white except for a characteristic yellow-brown breast, and the normally yellow breast of an "albinotic" meadowlark may be marked by a pure white crescent in place of the usual black one.

Yellow and Dominant White in Other Cases

One of the most striking examples of the relation of black, yellow and dominant white is presented by crosses where factors for black spangling are also present. In stock of this sort some birds are obtained with yellow and black patterns, and others with the same pattern except that the black is replaced by white (Figure 5). The latter breed as dominant whites.

Rhode Island Reds crossed to White Leghorns generally give chicks with much the same pattern and color as that of the F_1 light specimens in the present series, indicating that the red of the former involves both black and red-yellow as do our dark F_1 males (Cf. Agar[1]). In many heterozygous specimens with Rhode Island Red or similar ancestry the males show a definite tendency to have much black in the breast and



YELLOW FEATHERS WITH WHITE TIPS

Figure 5

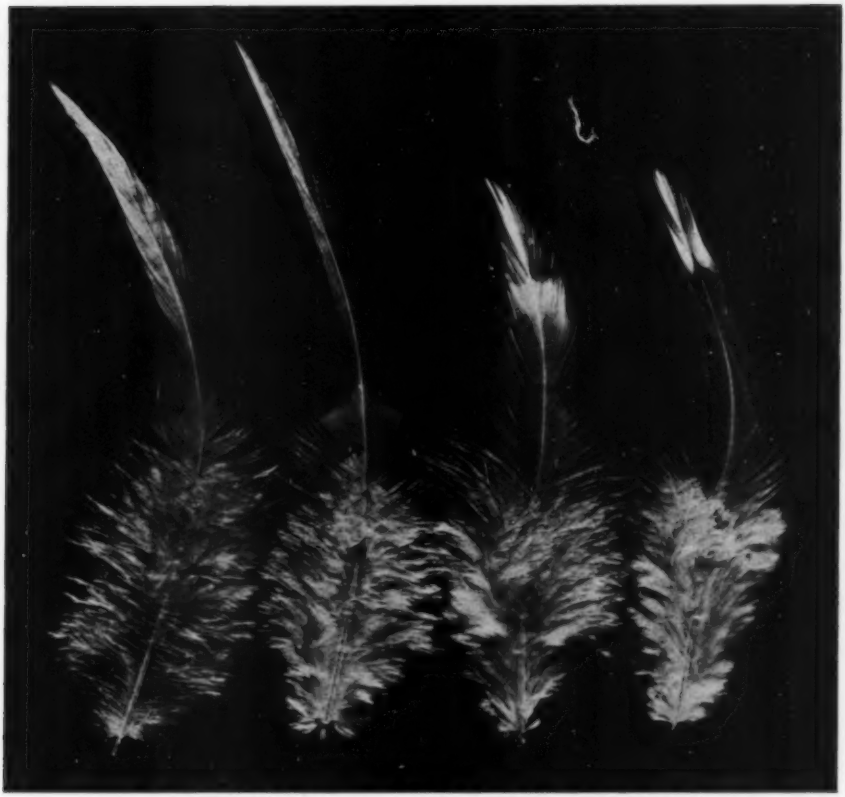
The white tip indicates a region which would have been black were it not for the presence of a gene for dominant white. The father of the bird from which these feathers came did not carry such a gene and produced only feathers which were yellow with black tips.

wings and a varying amount of red in the shoulders and saddle. Such birds, if at the same time heterozygous for dominant white, present a pattern often seen in mongrel stock —a pure white breast associated with more or less red in shoulders, hackle and saddle. Many of these, probably mostly the heterozygous ones, are closely similar to males described by Warren[12] as counterparts of salmon-breasted females that sometimes occur as a variant type of White Leghorn. Our data support Warren's conclusions as to the probable nature of these off-color birds.

Other writers, including Davenport, Dunn, and Serebrovsky, have pointed out that dominant white is not entirely epistatic to red and yellow. Results of our own matings indicate that the red or yellow in both the male and the female pattern may be only slightly reduced by the gene for dominant white when it is heterozygous, and often but little reduced even when it is homozygous. Many good White Leghorns are found on outcrossing to have the genotype for a kind of Dominique pattern and color without any red, even in the male (Cf. Hadley[7]). It is now clear that some such genotype is a desirable, if not an absolutely necessary, substratum on which to build a strain in which both sexes will have a pure white plumage with no trace of yellow or bronze markings. The desired genotype of a Red Pyle Game, which is apparently that of a Black-breasted Red plus dominant white, would consequently never do for a White Leghorn, in spite of the fact that both have the same genes for white.

Interrelation of the Genes for Black and Yellow

On studying the distribution of black and yellow or what amounts to practically the same thing, dominant white and yellow, it at once becomes apparent that the two contending genes in heterozygous individuals meet with varying degrees of success in different parts of the body. Black is almost certain to appear in the tail, if at all; and yellow, if it is to appear anywhere, is usually found on the breast of the female and the shoulders of the male. Other regions are yellow or black (white) depending on accessory factors. A number of investigators, including Zawadowsky[13] and Lillie,[9] have drawn attention to the difference in physiological threshold of feather follicles in different parts of the body. The parallelism between the location of the physiological threshold and the distribution of areas affected by genetic color factors is very close and suggests that the relation may be a fundamental one. It may be that the extension factor E^m (Dunn[9]) produces its effect through modifying



A "PROGENY-TEST" BY ENDOCRINE TREATMENT

Figure 6

These feathers show how the active principle of an endocrine may be used in lieu of a breeding test to determine a genotype. The two longer feathers at the left are from the yellow specimens described in the text. The two shorter feathers at the right are from the same two birds after they had been treated with tryroxin. The color of all of these feathers is exclusively yellow and buff except for a sub-terminal diamond shaped area on the feather to the extreme right. The test shows that one bird did and one did not carry a factor for dark pigmentation, and that they would consequently have behaved quite differently in a breeding experiment.

the reactivity of certain regions to the genes for black and yellow. If this should prove to be the case, we should be in a better position to study the time and mode of reaction of these genes.

The gene for dominant white (when present) comes into effect at whatever age and under whatever conditions yellow would be replaced by black. This is shown by comparing color development in properly selected individuals, and by direct experiments. For example, through intermittent use of thyroxin or theelin, the effects of the gene for dominant white may be thrown in or out of action within a matter of hours.

Relation of Genes to Endocrine Treatment

When a male with the black-breasted red pattern (Brown Leg-

horn) is given the correct dose of follicular hormone (Juhn and Gustavson[3]) he produces yellow-brown breast feathers. When the same treatment is given a Red Pyle male, which is similar except for the dominant white, he does likewise. But within forty-eight hours after the treatment is stopped, the developing breast feathers of the first male begin to produce black pigment while those of the second become pure white. If the treatment is resumed, however, both males again produce similarly colored feathers. A considerable number of experiments of this sort indicate that the gene for dominant white creates a condition which inhibits black pigment at the very moment when it is about to be formed, (Danforth[3]).

These endocrine tests may sometimes afford a quick method for determination of a genotype. For example, since the theelin and thryoxin tests have been found effective with Red Pyles, a breeder of White Leghorns could no doubt pick out young males carrying the "salmon-breasted" factor of Warren long before the trait could be detected somatically or by breeding tests. The results of an analogous test made on two buff specimens are shown in Figure 6. Both birds were developing new saddle feathers at the beginning of the test. On July 14, one of them weighed 2,410 grams, the other (younger) 1,140 grams. On each of the next four days the former was given 2.4 milligrams of Squibb's thyroxin by mouth, while the latter received 1.6 miliigrams daily for the same length of time. On September 12, an examination of the feathers revealed that the larger specimen was homozygous for pure yellow, while the other was of a genetic constitution to produce some daughters, at least, with much black in their plumage. The rationale of this test (which can be completed in less than three weeks at most) is dependent on the finding that dosages such as were used affect the form but not appreciably the color in birds with genotypes for pure yellow or black, but both form and color in those which are heterozygous for these traits. If the smaller specimen had carried dominant white hypostatically, the dark spot on the feather to the right would have been white.

White and Yellow with Reference to Age and Sex

In most genotypes involving black and yellow, but with the gene for dominant white superimposed, the young of both sexes are almost pure white, while the adult hens show some yellow wash and the adult males an appreciable amount of bronze, yellow or red. Since this yellow develops toward sexual maturity, and is more pronounced in the male, its appearance would seem to be conditioned by the "endocrine balance." This inference is supported by the fact that the male pattern is readily converted to that of the female by proper amounts of thyroxin or theelin. Nevertheless skin-grafting experiments show that within either sex the genotype is the differential factor in determining the presence or absence of yellow. Stated briefly, the following results have been obtained with grafts involving skin of the saddle region from different kinds of white fowl. Skin from genetically non-yellow individuals produces pure white feathers irrespective of the amount of yellow in the host. That from birds with the genes for yellow or "brassy" usually produces pure white feathers if grafted to a female host and partially yellow feathers if the host is a male of any genotype other than that for hen-feathering. It thus becomes apparent that the appearance, amount and distribution of yellow in the plumage of dominant white birds depends in the first place, and primarily, on the genotype of the individual, and in the

second place, if the genotype is favorable, upon the endocrine substances in circulation at the time the feathers are developed. Broadly speaking, the situation is clear, and simple; but an inviting field is suggested for a more precise analysis of the nature of genic and endocrinal reactions.

Summary

The gene for dominant white is not very effective in suppressing the yellow component in plumage of the fowl, and when the bird is homozygous for yellow the white may become hypostatic and fail to appear.

When dominant white is added to a genotype which provides for the appearance of both black and yellow, the black is almost completely suppressed, the yellow only slightly reduced.

Age and sex differences in the amount of yellow shown by dominant white birds are due to endocrine differences, but the latter factors are without effect except in the presence of an appropriately responsive genetic constitution. An appreciation of this type of relationship between genetic and endocrine factors seems to be fundamental to an understanding of a rather large group of phenomena.

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Genetics of Multiple Sclerosis

MULTIPLE SKLEROSE UND ERBANLAGE, *by* Priv.-Doz. Dr. Friedrich Curtius. Pp. 215, with 17 illustrations and numerous pedigrees. Georg Thieme Verlag, Leipzig, 1933.

Curtius presents pedigrees and extensive statistical data showing the occurrence of some forty nervous diseases among the relatives (totaling 2,778) of 56 patients suffering with multiple sclerosis in various hospitals in Bonn, as compared with the incidence of the same diseases in the families of 56 fracture cases which were similarly investigated as a control group. For further comparison,

data concerning disease incidence in an "average population" of 200 families studied by Schulz and Luxenburger in 1927 and 1929 are cited, and the author's Bonn material is supplemented by clinical histories drawn from 50 other multiple sclerosis cases into which it was not possible to conduct so extensive an investigation.

The relatives of the multiple sclerosis patients show a strikingly higher incidence of psychopathic and neuropathic conditions than is found in the control groups, and the proportion of such affections is higher among the nearer than among the more remote relatives. A classification of the diseases considered into those which are presumed to be predominantly conditioned by heredity, partly conditioned by heredity, and chiefly or exclusively conditioned by environment, reveals the greatest difference in incidence between the relatives of the sclerotics and the control groups in the case of the partly hereditary diseases, lesser difference in the case of the partly hereditary diseases, and no perceptible difference in incidence for conditions which are attributed wholly to environment. Cousin marriages are about 4½ times as frequent among the parents of the multiple sclerosis patients as in the general population, but the number of cases is not large enough to establish statistical significance for this indication of recessive heredity.

The findings are interpreted from the viewpoint of "Konstitutionspathologie," and the author concludes that there is an hereditary constitutional type which is predisposed to affections of the central nervous system, of which multiple sclerosis is one manifestation, and also perhaps to other pathological conditions, such as the allergies. As the author points out, the maintenance of this thesis does not, of course, deny the possibility that the immediate etiological factor of multiple sclerosis may be a bacterial infection, susceptibility to which is determined by inherited constitution. Curtius does not commit himself to any simple factorial interpretation for the transmission of the diathesis, but does consider various theoretical possibilities, such as polymerism, multiple allelomorphism, and the variable expression of a single factor under different environmental conditions, which might be adduced to explain the situation.

Points which might be open to question are unavoidable in this type of study, and they are not absent here: one finds among the tabulated diseases, most of which are definite clinical entities, such vague rubrics as 'Psychopathie"; the attempt to classify nervous diseases according to the extent to which they are conditioned by heredity is one which is necessarily, in the present state of our knowledge, in large part a matter of conjecture; and some phases of the statistical treatment might be subject to criticism. It is unlikely, however, that any of these doubtful points are sufficient to invalidate the major thesis of the work. Much more serious questions arise concerning the collection of the data themselves. Were, for example, inquiries into the family pathological histories made with equal assiduity in the case of the control groups as in that of the multiple sclerosis families? Were the former equally as cooperative in giving information concerning neuropathic taints as were the families which had members already hospitalized with a serious nervous affliction?

A negative or uncertain answer to either of these questions would go far to account for the direction in which the data point. Granted the absence of any such bias in the data, however—and it must be admitted that every effort appears to have been made to avoid it—the arguments based on the findings seem to be essentially convincing. The author has made a significant contribution to the fields of constitutional pathology and human genetics.

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VON RECKLINGHAUSEN'S DISEASE

An Inherited Form of "Elephantiasis"

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OVERGROWTH OF THE NERVE FIBERS

Figure 7

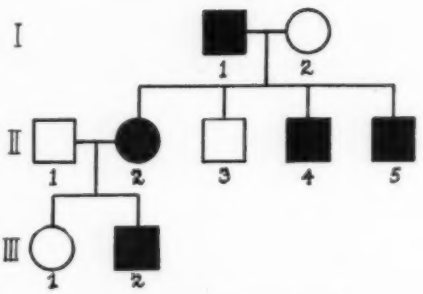
This mass of tissue is due to an inherited tendency to excessive proliferation of the peripheral nerve fibers and the nerve sheath surrounding them. The hereditary nature of the disease was established by a German physician, Von Recklinghausen, in 1881. The father of this individual, while he did not suffer from "elephantiasis" had many small fiberous tumors on his body, and his skin had the pigmented spots which are characteristic of the disease. Photograph courtesy of Dr. F. P. Anzinger.

A TEXT for a sermon on the way that genes and other forces which control our development interact in the production of an individual human being might be taken from that rare and tragic inherited disease named after a German physician, Von Recklinghausen, who described the condition in 1881. The inheritance, as will be shown below, is with some few exceptions that of a typically dominant character. We are probably correct in assuming that the occurrence of this unfortunate condition is governed by one of those important but ultra-microscopic particles which geneticists call a gene. It is true enough that the evidence of the gene-controlled nature of this condition is hardly proven with that conclusiveness which a student of the freely-reproducing Drosophila would demand. We have no crosses to test linkage,—no chromosome maps to prove where the iniquitous Von Recklinghausen gene is located. But we do have the fact that in a large number of cases the proportion of affected children of one affected parent is close to fifty per cent, as is expected in random segregation of a dominant character. Preiser and Davenport[6] completed an extensive study of the inheritance of this disease in 1918. They list such an imposing mass of evidence that its hereditary nature can hardly be questioned.

The next point to be taken into consideration in connection with this condition is the embryological history of two important elements of our body, the skin which covers us, and

the nervous system which tells us so much about the external world that mere skin could never tell. These two all-important parts of our bodily economy have a common origin. The beginning of the nervous system in the embryo is represented by a longitudinal groove in the "embryo skin" or ectoderm. This neural groove becomes enfolded in the developing individual and forms the beginning of the entire nervous system. Thus our skins and our brains are embryologically brothers (or cousins), as we might say, having a common origin in the ectoderm of the embryo. This fact is possibly connected with the observation that the symptoms which characterize Von Recklinghausen's disease show their major manifestations in the nervous system and in the skin. The neural symptoms, an overgrowth of the peripheral nerves and the connective tissue of the surrounding nerve-sheath, are more striking than the deeply pigmented freckles and spots on the skin which characterize practically all individuals having such tumors. Furthermore, the regions of these fibrous tumors are more deeply pigmented than the normal skin (see Figures 7 and 9).

There are some curious and possibly important connections between hyper-development of pigment in the skin and tumor formation. In this instance we have an apparent instability in the pigment- forming mechanism accompanied by tumors of the sheaths of the nerve fibers. Attention has been called in the Journal before to the tendency of pigmented spots on white horses to form benign tumors of another type, the so-called melanomas.[3] Gordon, in his very interesting and important studies of tumor formation in hybrid fishes reported in this Journal and elsewhere,[2] discovered a situation in which abnormal pigment formation resulted in tumors of a definitely malignant type. While Von Recklinghausen's disease is not generally classified as a cancer because it does not "metastisize"



THREE GENERATIONS OF "ELEPHANTIASIS"

Figure 8

Inheritance of Von Recklinghausen's Disease in a family reported by T. Carwardine in 1899. The affection does not skip a generation and affected individuals have both normal and affected children in about equal numbers. From this and other evidence it is concluded that Von Recklinghausen's Disease is inherited as a dominant characteristic.

to other organs of the body, still it has much in common with the cancers and may be regarded as an intermediate form between normal and malignant cell development. A more intensive study of the non-malignant tumors may throw further light on the causes of cancer and its inheritance.

Tendency toward the inheritance of tumors of the peripheral nerves was noted as long ago as 1847 when Rudolph Virchow, the father of modern pathology, recorded the inheritance of such tumors for three generations in a father, his son, and in the grandchildren. In 1899 T. Carwardine recorded the inheritance of fibromas for three generations (Figure 8). The individual designated *III-2* when twenty-five years old "was covered with nodules of various size, some deep seated, and a pendulous fibroma upon one buttock. Several pigmented patches and a multitude of freckles. *II-2* was similarly affected." Von Recklinghausen, after whom the disease is named, called attention to its heritable nature in 1881; and

PIGMENT FORMATION AND TUMOR DEVELOPMENT RELATED

Figure 9

Note that the region of excess growth is more heavily pigmented than the skin over normal tissue. This photograph is reproduced through the courtesy of Dr. F. P. Anzinger. Copyright by American Medical Association.

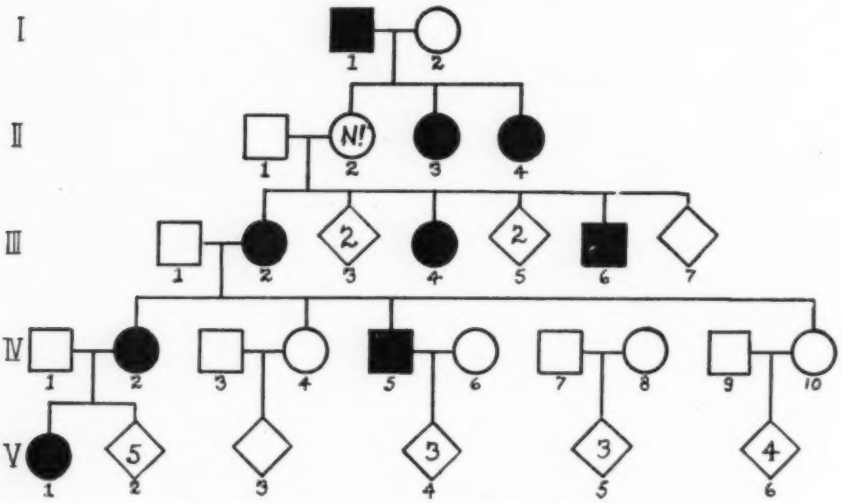
in 1898 he made a clear distinction between these tumors and true neuromata (tumors of the nerves) in the following terms: "The essential feature was an outgrowth of the connective tissue envelope of the nerve bundles and of the endoneurium . . . . . the term neuroma should be restricted to tumors formed of proliferative nerve cells." He concludes that the tumors appearing in this disease should be classified as neuro-fibromata because they are made up as much of connective tissue as of nerve tissue. The overgrowth of tissue typical of this disease arises from nodules of nerve and connective tissue which may be spread all over the body, as many as four thousand of these tiny tumors have been counted in a single individual. Why some of these tumors remain in this "preliminary stage" and why others develop into larger masses is not clearly understood.

In the pedigree recorded by F. Harbitz in 1909, inheritance of "elephantiasis" is recorded for five generations. The individual designated *V-1* in the chart (Figure 10), when twenty-five years old showed an elephantiasis of the left leg due to confluence of fibro-neuromata and similar conditions have existed in other members of the family as shown in the chart.

This form of "elephantiasis" is to be definitely distinguished from true elephantiasis which is caused by a parasitic organism and which is carried from host to host without benefit of heredity.

Another hereditary form of "elephantiasis" was illustrated in the Journal some months ago. This form called Milroys disease[4] is limited to the lower limbs. The overgrown limbs are not the result of tumor-development, but appear to be due solely to a weakness of certain tissue elements. The external appearance of the two conditions might, in some cases, be quite alike, but their cause is entirely different.

The early evidence of the condition



INHERITANCE FOR FIVE GENERATIONS

Figure 10

This chart showing five generations of the inheritance of Von Recklinghausen's Disease was published in 1909 by F. Harbitz. The two pedigrees reproduced here are representative of a great many that have been published demonstrating the heritable nature of this disease. They show the characteristic direct inheritance and segregation of normal and affected individuals in the progeny. Occasionally the condition skips a generation as in generation II in this family but apparently in all these instances the "carrier" who transmits these tumors without having them has the typical pigmented spots on the skin. In some cases apparently an external stimulant such as a bruise is necessary to initiate the formation of excess tissue.

consists of pigmented spots on the skin and local bunches of tissue which were not especially painful to the touch. The father of the individual shown in the accompanying illustrations had only the spots and multiple fibrous growths over his body. The latter did not develop to any such great extent as those which made their appearance in his son.[1] The two brothers of the boy had pigmented spots on the body but no tumors. One sister has the spots while one is without them.

It is altogether possible that some external stimulation is necessary to bring on the development of these fibromas. In a case recently reported,[5] the formation of a large tumor on the face followed a blow with a baseball. It was further aggravated by an attempted extirpation, which in these cases apparently can lead to only the most serious consequences.

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PSEUDOGAMY IN BLACKBERRY CROSSES

So-called "False Seedlings" Produced in Hybrids between European and American Varieties

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EUROPEAN blackberries differ from American blackberries in that many, if not all, may reproduce the parent exactly when grown from seed while no American varieties have been known to do this.* According to Gustafsson[6] such seedlings are pseudogamic in origin.

In cases of pseudogamy the flowers must be pollinated to stimulate seed development but there is no evidence of any effect other than of the pollen parent in the resulting seedlings. Some European forms of blackberry may produce a hundred per cent of such pseudogamic seedlings, others produce many true seedlings as well as a large proportion of the false seedlings, and still others produce all true seedlings.[7] Gustafsson thinks pseudogamy has arisen in European blackberries through crossing between very different species groups. He thinks it is recessive and occurs where the factors for it have come together since Pliocene times, and the resulting forms have survived and reproduced by pseudogamy, some of them for ages.

Two European varieties are of commercial importance in the United States. These are the Oregon Evergreen (*R. laciniatus*) widely grown in Western Oregon and Washington, and the Himalaya (*R. procerus*) grown in California as well as in Oregon and Washington. Both species are being used in breeding and already one promising new variety, the Brainerd, has been introduced, of which the Himalaya was one parent.[5] Both the Oregon Evergreen and Himalaya may reproduce true from seed and the Oregon Evergreen has been sometimes raised from seed commercially.[2] They have become naturalized so extensively in the Pacific northwest that fruit is gathered in immense quantities from wild plants. Because of their great vigor and thorniness they are becoming a serious pest in that region in pastures and along the highways.[4] In New Zealand naturalized European blackberries are an even more serious pest. Because of these considerations this method of reproduction of European blackberries by pseudogamy and some results when crosses are made with American varieties are reported here.

C. E. Schuster has tested the Oregon Evergreen for pseudogamy. He found that unpollinated emasculated flowers produced no seed while pollinated flowers regularly set seed and reproduced the female parent exactly. This agrees with the work of Lidforss[7] and Gustafsson on European blackberries in Europe.

Although in the wild state where they are usually self-pollinated, these European varieties usually reproduce by pseudogamy, it does not necessarily follow that when emasculated and pollinated with pollen of American varieties they produce an equal number of false seedlings. Several years ago an indication of such a difference was obtained when the senior author raised several hundred selfed seedlings of the Oregon Evergreen, Himalaya, and Edward Langley (another European variety). All of these seedlings were apparently pseudogamic. However when flowers of the Oregon Evergreen were emasculated and pollen of the Himalaya used, two true crosses out of about ten seedlings were obtained.

* A possible exception is the form of *R. canadensis* studied by Brainerd and Peitersen[1] which they reported to show no segregation. Seedlings of it which we have raised but not actually selfed show remarkable segregation.

In 1932 the authors were able to obtain further evidence on this point. Crosses were made between Oregon Evergreen and Himalaya as mother parents and the American varieties Taylor, Kittatinny, Early Wonder, Snyder, Lawton, Joy, Austin Thornless and Eureka as pollen parents. Table I gives a summary of the records obtained at the U. S. Department of Agriculture Field Station near Glenn Dale, Md., and at the Coastal Plain Station of the North Carolina Department of Agriculture at Willard, North Carolina.

The total numbers for the Himalaya and Oregon Evergreen crosses are large enough to be significant though many of the individual crosses are not. In general they indicate that about one-tenth of the Oregon Evergreen crosses and one-third of the Himalaya crosses may be expected to be true seedlings and nine-tenths and two-thirds to be pseudogamic seedlings. Where the numbers in the different crosses are large, as in those of Himalaya with Taylor and with Kittatinny, the ratios are relatively close to that for all crosses. Where the numbers are small the ratios vary widely. In the cross of Himalaya × Eureka eight out of the ten were true crosses. Though the numbers are too small to be significant it recalls the suggestion of Lidforss[7] that if the parents are closely related, true and false hybrids occur in about equal numbers. It is of interest to note that Eureka is a variety of *R. cuneifolia,* the sand blackberry of the Atlantic Coastal Plain region which is nearest related to the European species and, in its pinkish flowers, late blooming, extreme thorniness, white tomentum of the under surface of the leaves, etc., shows a connection in recent ages with them. It may possibly represent the European type before European species were pushed southward in the ice age and when it is supposed they were mixed with tropical or southern forms and pseudogamy appeared.

The cross of Himalaya × Oregon Evergreen gives very close to one-third true crosses and two-thirds pseudogamic seedlings. These varieties each have the same chromosome number, 14 (=1*n*), while counts by A. E. Longley indicate that the American varieties Taylor, Early Wonder, Snyder, Joy, and Lawton also have 14, the Eureka 7 and Austin Thornless 28 chromosomes.

Three seedlings are listed in the table as doubtful. The two doubtful seedlings of the Oregon Evergreen are like Oregon Evergreen except that they are broad-leaved, of the type that grows wild in some parts of Oregon and Washington and which there reproduces by pseudogamy. Possibly the broad leafed forms have originated as seed sports of plants reproducing by pseudogamy.

The seedling of Himalaya × Austin Thornless listed as doubtful is a thornless seedling which appears identical with the pollen parent. It is the first instance noted by the writers which suggests paternal inheritance in Rubus although Lidforss reported similar paternal inheritance. Several of the true crosses are thornless, apparently thornlessness being partially dominant in the Austin Thornless though in other varieties of Rubus it is recessive to thorniness.

It is of interest to note that seven species of citrus are reported[8] to reproduce by apogamy giving from 10 to 100 per cent apogamic seedlings while six out of seven hybrids between citrus species give 100 per cent apogamic seedlings. The seventh hybrid developed few if any apogamic embryos and broke up in the F_2 generation. Although citrus species are diploid there is suggested a remote hybrid origin of the species themselves.

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TABLE I.—Numbers of pseudogamic seedlings and true seedlings resulting from blackberry crosses..

Cross	*False Seedlings*	*True Seedlings*	*Doubtful*
Oregon Evergreen × (an American variety)	71	9	2
Himalaya × Taylor	132	60	-
" × Kittatinny (? identity)	62	44	-
" × Early Wonder	16	21	..
" × Oregon Evergreen	22	14	..
" × Snyder	27	7	..
" × ———(An American variety)	25	3	..
" × ———(A second Amer. var.)	12	3	..
" × Lawton	9	8	..
" × Joy	9	6	..
" × Austin Thornless	13	9	1
" × Eureka	2	8	..
Total Himalaya seedlings	329	183	3
% " × American	64%	36%	
% Evergreen × American	89%	11%	

"Metronome" Genes

DAS PERSONLICHE TEMPO. Eine erbbiologische Untersuchung. *By* IDA FRISCH-EISEN-KOHLER. 63 pages, 10 figures. Georg Thieme, Leipzig, 1933.

THIS small monograph, coming from the Kaiser Wilhelms-Institute for Anthropology, Human Genetics and Eugenics in Berlin-Dahlem, seems likely to become the starting point for a new and interesting field of research in human genetics. In studying the "personal tempo" of different individuals, two types of experiments were used for analysis. In the tapping experiments the person to be tested was asked to tap with his hand or a finger on or against a table (no particular way of doing this being specified), or the person was asked to tap with the stretched-out index finger against the edge of a table, or to tap with the foot on the floor. The tapping was to be done at the most agreeable speed. The second type of experiment was carried out with the help of a metronome. The metronome was run at different speeds, the person to be tested being asked at each one whether it was too slow, too fast or just right for him. In a second series of trials the person was asked to determine which of several speeds of the metronome impressed him as neither slow nor fast. The experiments demonstrated that one and the same test applied to an individual at different intervals gave almost identical results. Neither the time of the day nor the individual's mood or physical condition appeared to influence the outcome of the test to an appreciable degree. The coefficient of correlation of the results of the different types of tapping tests was very high and positive, the lowest being 0.92 ± 0.04; the same high correlation was found between the

two kinds of metronome tests. On the other hand, a comparison of the results of the tapping tests and of the metronome tests gave a less striking agreement.

The metronome tests probably give the more exact results. Age (between the ages of from six to seven to over sixty years) appears to have no appreciable influence on the personal tempo. The personal tempo of males on the average was somewhat slower than that of females; the differences, however, are not statistically significant. Social environment does not seem to play a rôle. These conclusions are based on a study of a group of 456 grammar and high school children (equal number of boys and girls) of between about 7½ and 17½ years of age, and of smaller groups of adult persons of various occupations. The next step was taken with a study of 118 pairs of twins (26 identical male and 27 identical female twin pairs; 25 non-identical male, 24 non-identical female, and 16 heterosexual twin pairs). The tests on this material yielded striking differences according to the closeness of genetic relationship between the compared pairs. This is best shown by the results of the metronome tests, the average percentage deviations between the individuals of pairs (without regard to sex) being as follows: Identical twins 7.8, non-identical twins 15.5, sibs 15.4, unrelated individuals 20.6. On the whole, Frau Frischeisen-Köhler's material undoubtedly provides strong evidence for the conclusion that there is a genetic basis for individual differences in personal tempo. Finally, a study was made of 85 families with a total of 318 children. The following table illustrates the most important results of this investigation (see below*).

The results of the different matings represented in this family material cannot be explained on the basis of differences in one gene pair only. Sex-linked inheritance apparently does not play a rôle. Frau Frischeisen-Köhler believes that her results can best be explained by the assumption of two pairs of multiple allelomorphs with dominance of the more rapid personal tempo. Relations probably exist between the personal tempo as defined by these tests and other physiological facts (heart rate, respiration), and any agencies which upset the latter (e.g. endocrine disturbances) may influence the personal tempo. This remains to be investigated, as also racial differences. The simplicity of technique and the surprisingly low variability in individual expression of this character highly recommend it for further study.

WALTER LANDAUER.
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*Pairs of parents	Number of children	If the tempo of both parents is	Then, the tempo of per cent. of the children is		
			Fast	Medium	Slow
8	25	Fast	56.00	40.00	4.00
25	99	Medium	17.17	65.66	17.17
8	28	Slow	.....	28.57	71.43

Hereditary Eye Disease

At the meeting of the Japan Ophthalmologic Society recently in Tokyo, Prof. Dr. B. Hata, of the Okayama Medical University, reported that since 1928 he had examined about 25,300 cases of eye disease, among which he found 311 cases of malignant pigment degeneration of the retina, a kind of cataract that begins at adolescence with night blindness, and ends in blindness in a score or so of years. Among the 311 there were 161 blind. Going back to their ancestors, he investigated the relation of this disease to marriage and heredity. Fifty-four cases were found to have occurred among consanguineous marriages. Of these fifty-four patients, forty-four had parents who were related by blood; 167 had ancestors who had suffered from the same disease. No such transmission was found in forty-four cases. He concluded from this research that the disease was transmitted by intermarriage or was hereditary.—*Jour. Amer. Med. Assoc.*, July 25, 1933. p. 225.

FISH HYBRIDS AND FISH GENETICS

MYRON GORDON

A PAPER entitled "The Involved Genetics of Fish" by A. Brazier Howell[1] has recently appeared in *Science*. It contains a discussion of a previously published report by C. L. Hubbs and L. S. Hubbs[2] on "Apparent Parthenogenesis in Nature, in a Form of Fish of Hybrid Origin."

In illustration of some of his points Howell mentions results which he has obtained in hybridization of the platyfish (*Platypoecilus maculatus*) with the swordtail (*Xiphophorus hellerii*). It is only Howell's conclusions concerning his own work on the hybridization of these two genera of fishes and his implication that the phenomena displayed in ichthyological genetics are complicated that I wish to discuss.

With regard to the implied confusion that exists in our knowledge of the genetics of fishes it may be said that a certain amount of complexity might be expected when an attempt is made to analyze the results of generic crosses. Generic crosses in other animals and plants are also somewhat complex. Nevertheless the papers of Gerschler[3], Kosswig[4], Haussler[5], Gordon[6] and others (see bibliography, foot note 6) furnish working hypotheses for the results obtained in the crosses that Howell mentions. But when intervarietal crosses are made in any of the species studied such as *Oryzias*[7, 8, 9], *Lebistes*[10, 11], *Platypoecilus*[12, 13, 14, 15], the laws of inheritance are followed closely and without undue complexity. To be sure, an unusually large proportion of the genes in the species of fishes studied are sex linked. It is true, also, that both types of sex chromosomes of fishes carry dominant genes and there is much evidence to show that these sex-linked dominant genes occasionally cross over. Furthermore, some species of fishes in a sub-family (*Poeciliinae*) have the *XY* type of sex inheritance, others have the *WZ*. These phenomena give the subject of fish genetics added interest but they are not particularly involved.

In explanation of the occurrence of females only in the natural hybrids of *Mollienisia formosa* Howell offers observations on the sex ratio found in the yellow mutant stock of *Xiphophorus hellerii*, the swordtail. The "golden swordtails consistantly produce two to three times as many females as males, and the case of *Mollienisia* may be an instance of this factor carried to an extreme." In this connection perhaps the suggestion of Kosswig[16] may be helpful. The latter has indicated that certain genes for color are closely associated with genetic factors influencing sex. It must be stated, however, that Kosswig has not mentioned the golden mutant.

Further points made by Howell require reviewing in the light of previously published accounts relating to the platy-swordtail hybrids. I refer to his comments under the heading of 'c':

> The matroclinous character of the offspring can involve no argument in favor of parthenogenesis, for I can cite reverse evidence, of a patroclinous nature as follows: I have a strain of hybrids produced by crossing a male black platy (*Platypoecilus*) with a female of the golden swordtail strain of *Xiphophorus* which are large, spectacular fish, mostly black but with many spots and blotches of green and orange. Apparently all individuals of this hybrid or at least a large proportion of them, are fertile, and when bred to one another they behave as a true species. In other words all the young of the second generation resemble their parents rather than either of the grandparents. So far so good, with nothing very remarkable.

But this is remarkable. Are these *Platypoecilus-Xiphophorus* hybrids comparable to Karpentchenko's *Brassica-Rhaphanus* true breeding types? If so, the importance of these platy-swordtail hybrids cannot be overestimated. The results of other investigators[4, 6, 17] with respect to the behavior of these fish hybrids in the second generation

indicate a segregation for both size and color pattern factors. It is suggested that the second generation hybrids of Howell's, although all dark, (three-quarters are expected to be dark) may be segregated, eventually, into separate groups.

Howell's results in obtaining seemingly patroclinous inheritance in the back cross of a hybrid (black platy × gold swordtail) male to a pure green swordtail, as mentioned above, are at variance with results of investigators working with green swordtail stocks. In the latter case it has been found that when a first generation hybrid carries any of the dominant color genes contributed by platy parents such as *red, spotted black, one-spotted, crescent,* and is crossed back to the swordtail species, the various color genes segregate approximately in the proportion of one to one. The results of Howell given by him in an earlier paragraph to the effect that in back-crossing of a black platy-swordtail hybrid female to a pure swordtail male, he obtains approximately three-quarters of the resultant young as colorless (not black) like their father, and one-quarter black like their hybrid mother, indicate to me that these are aberrant results and may probably be attributed to chance. The significant one-to-one back cross ratio would probably appear if sufficient young were observed whether the hybrid tested were male or female.

The facts concerning the genetics of the platy-swordtail hybrids are not applicable to Hubbs' case in *Mollienisia.* As I understand the latter situation, the important point about the hybrids, *M. formosa,* is not so much that they exhibit matroclinous inheritance for a particular color gene but that they exhibit matroclinous inheritance for all the morphological features of the body. It is well known in *Lebistes*[10] that certain stocks of males transfer their color patterns to their sons only. In certain stocks of *Platypoecilus,*[18] females transmit their dominant color patterns to their daughters only. In *M. formosa* we are not concerned with a few genetic differences but a complexity of genetic factors affecting all parts of the body.

It is highly desirable that the hybrids which Howell has obtained should be studied further. This it may be possible for me to do, as Howell has kindly offered me the necessary material.

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Pure-Bred Sires

Establishing a new high figure of 18,037 in total registrations, the "Better Sires—Better Stock" campaign, sponsored by the Bureau of Animal Industry, United States Department of Agriculture, is staging a come-back from the depression. Most of the States are now enlisted in the better-sires campaign, the entrants pledging themselves to use only pure-bred sires on their farms. This applies to livestock of every kind, including poultry.—*U. S. Department of Agriculture Clip Sheet.*

A "BUFFALO" CALF

L. J. HORLACHER

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WHENCE THE BISON-LIKE APPEARANCE?

Figure 11

THIS "buffalo" calf is out of a purebred Jersey cow and by a purebred Shorthorn bull. It was born April 1, 1932, on the farm of A. C. Savage of Maysville, Kentucky. At nine months of age the calf was 3 feet, 11 inches long, 2 feet 4 inches high, 5 feet in girth, and weighed 250 pounds. It is a female with apparently normal development of external genitals and has shown some signs of heat.

The calf has always had long hair, with an especially long tuft under the brisket and on the lower part of the neck. The head is peculiar and not like that of a normal calf. It is dished between the eyes and is large and rounded at the upper part. The lower jaw is long and heavy and the nose is slightly turned up. The teeth are large and slightly proturding. The eyes are very large. The horns are set on top of the head, close together, with a tendency to turn down and out.

The calf seems to be healthy and it requires very little feed. It is playful in a quiet way and shows plenty of bovine intelligence. It has been fed and handled along with the other calves on the farm and thrives on less feed than is required by the average calf. When its mother was fresh the calf nursed only one teat. The owner plans to take good care of the calf, grow it to maturity, and if possible, breed it. In the meantime it will be kept under observation by the Department of Animal Husbandry of the University of Kentucky.

AUTHOR'S NOTE: The calf died at the age of exactly ten months. A post mortem examination was held at the University of Kentucky and as a result of the examination the calf was classified as a typical cretin dwarf. The thyroid gland was about one-third normal size. The large stomach, pug-nose, and short crooked legs were of the type common in the cretin dwarf.

PLANT GENETICS IN 1932

A Review

RECENT ADVANCES IN PLANT GENETICS, *by* F. W. SANSOME and J. PHILP. Foreword by Sir Daniel Hall. Pp. x + 414. 56 figures, 42 tables. Price, $4.00. P. Blakiston's Son and Co., Philadelphia, 1932.

THIS publication contains an excellent account of the recent work in plant genetics, and shows the rapid strides which are being made in this field.

Considerable space is devoted to the recent cytological advances. In considering the cytological basis of genetical crossing-over and related questions, particular attention is paid to the views put forward by Darlington, who is, like the authors, a research worker at the John Innes Horticultural Institution. The authors' treatment of this controversial field is interesting and stimulating, although doubtless many will disagree with some of their conclusions. Nine linkage groups are listed for maize. Apparently the authors are unaware that the general practice among corn geneticists is to number the linkage groups according to the size of the chromosomes upon which they are borne, chromosome one being the longest and chromosome ten the shortest. The remaining linkage group (there are ten pairs of chromosomes in maize) is now known. The corn geneticists have set up an excellent example and deserve much credit for the fine spirit of cooperation which they show in freely exchanging material and unpublished data. As a result there are many important findings which are common knowledge among the workers in this field but which have not appeared in the literature yet, and are consequently unavailable to others. In spite of the book's title, frequently it has been necessary to refer to the Drosophila studies. This has been done in comparing genetical and cytological maps of the chromosomes. The studies now being carried out with maize are yielding results which will make possible in the near future a similar comparison of genetical and cytological maps for a plant species.

In discussing the constitution of the factor (gene), the inadequacy of the original presence and absence hypothesis is pointed out. Eyster's genomeric hypothesis, the step allelomorph concept of Serebrovsky and co-workers, Thompson's side-chain hypothesis and Goldschmidt's physiological hypothesis are reviewed. Fisher's theory of the evolution of dominance is presented, but no mention is made of the work of Sewall Wright or Haldane. The authors wisely conclude that as yet we have comparatively little knowledge of the nature of the gene itself. Recent attempts to estimate the size of the gene, and to calculate the number of genes borne on the chromosomes, are not treated.

Origin of Polyploids

Many pages are devoted to polyploidy and related phenomena. Polyploids may originate through the doubling of the chromosome number in somatic tissue, or through the formation of gametes containing either the unreduced number of chromosomes or at least more than the haploid number of chromosomes. It is pointed out that the genetical consequences of these two methods of doubling may be different since doubling in the somatic tissue introduces no qualitative difference in factor content, but only a quantitative difference between the original and its derivative tetraploid form. Abnormalities in gametogenesis are grouped under four heads: where the first or second meiotic division is nullified; where the chromosomes divide equationally twice; syndiploidy or the formation of binuclear germ cells; where the first division is completely suppressed. In an autotetraploid the four homologous chromosomes can pair with one another and assort at random to each pole. The resulting genetic behavior is

treated fully in this text. In an allotetraploid the chromosomes are derived from two or more plants of dissimilar origin, and the degree of similarity between these two or more kinds influences the manner of pairing and disjunction of the chromosomes. In some cases pairing takes place only between chromosomes of the same phylogeny (autosyndesis) but in other cases the pairing may be between chromosomes of different phylogeny (allosyndesis). The genetical consequences of these types of chromosome behavior are discussed, and the evolutionary significance of allopolyploidy is emphasized. A chapter is devoted to the origin and genetical and cytological behavior of triploids and haploids, and to primary, secondary and tertiary trisomics, especially in Datura. In a chapter entitled "Structural Hybrids," chromosome ring formation in a number of plant species is considered, and recent work with Oenothera is reviewed.

Interspecific hybrids in *Galeopsis, Triticum, Nicotiana, Crepis, Viola,* and *Antirrhinum* are dealt with. The results which Baur obtained with *Antirrhinum* are contrasted with those obtained in such genera as *Crepis, Nicotiana* and *Viola* which contain species whose evolution is bound up with chromosomal change either in number or structure. The reviewer was recently told that our American species of *Antirrhinum* differ from one another in morphological characters to a much greater extent than do the European species which Baur studied. A study of American *Antirrhinum* species should prove immensely profitable and perhaps would yield results differing markedly from those obtained by the European investigators.

It is inevitable that in a field like plant genetics, where papers are being published in a continuous stream, a book will be out-of-date in some respects almost as soon as it appears in print. For the same reason, a résumé of recent work is of great benefit to the research worker who is hard pressed to keep up with the literature. The authors' discussion of many of the largely unsolved problems attracting wide attention at the present moment is interesting and stimulating. The book will repay careful reading and is a useful addition to the geneticist's library. A long and imposing bibliography adds to its value.

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The Human Ovum

L'OEUF HUMAIN ET SES ANNEXES, *by* MAURICE LUCIEN ET HENRI VERMELIN. G. Doin & Cie, Paris, 1933.

THIS book presents little that is very new, and not much that is really antiquated. Some readers will dissent from the authors' opinion that in man, as contrasted with other mammals, maturation of the ovum is completed within the ovary (p. 19). The occurrence of an occasional ovarian pregnancy hardly justifies such an assumption. Another view that will not meet with universal assent is that ovo-genetic activity of the germinal epithelium is limited to an "eminently transitory" period in fetal life (p. 12) and that at birth the ovary contains all the ova that will ultimately be matured. There are investigators who believe that at birth the ovary contains no definitive ova. In discussion of chromosomal relations, the scheme of Winiwarter and Oguma, which postulates an *X-O* formula for the male, is presented rather fully although reference is made to studies of Painter which indicate an *X-Y* formula for the human male.

It possibly should be pointed out that the word *ovum* (oeuf) is used in the clinical sense to indicate not merely the female gamete (Fr. *ovule*) but also the developing embryo and its membranes. This usage can be justified since the bird's egg, to which the term ovum was probably first applied, is ordinarily

a muticellular structure. It is of passing interest that in many mammals the female gamete never appears in the form indicated in the diagrams (which correspond to those of most similar books) inasmuch as it is not the ovum but the secondary oocyte which is entered by the sperm cell. This is the case in mammals where the facts are definitely known but, as indicated above, Lucien and Vermelin question its universal validity in man.

In the sections on development, the discussion of twinning will probably be of most interest to geneticists. According to the authors twins are of just two types: the biovular, developed from two eggs fertilized by two sperms, and the uniovular, from a single egg fertilized by a single sperm. They take no stock in two-headed sperms, binucleated eggs or double fertilization as causative factors in twinning. They believe that only normal gametes are capable of producing viable embryos. The possibility of biovular twins having different fathers (super-fecundation) is admitted, but no valid ground is recognized for supposing that super-fetation (re-impregnation during pregnancy) ever occurs in man. However closely the placentas of two biovular twins may be pressed together in the uterus, they never really fuse or show any vascular union. In this respect man differs from some of the ungulates. But in the common placenta of two uniovular twins vascular anastomoses are characteristically present. When the connections between the two sets of arteries and veins are not such as to give a balanced circulation, one of the twins (the "transfusor") may pump a disproportionate amount of blood over to the other one with occasionally disastrous results to one or both—a point of some interest in the "nature-nurture" problem as it relates to twins.

Most of the book, dealing as it does with ovarian, uterine, and vaginal cycles, the time and conditions of ovulation, and development of the embryo, is not of primary genetic interest. But embryology is of ever increasing importance to the student of heredity, and this volume will serve well as an introduction to this field and to some subjects in which the embyrologist is especially interested.

C. H. Danforth.

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The Twins of the Father

MULTIPLE births in humans is a subject of never-failing interest. The existence of two sorts of twins—fraternal and identical—is now well recognized but the causes of twinning are still a matter for debate. Although we are accustomed to shower hearty congratulations upon the father of twins, most investigators have concluded that the production of twins is an hereditary attribute of the mother.

As early as 1920 Dr. C. B. Davenport presented evidence to show that fathers of twins actually deserve some of the credit they receive. In response to criticism of his conclusion Doctor Davenport delved further into this subject with the result that his convictions were strengthened.*

From a study of two hundred families involving 865 multiple births he shows that the influence of the father in the production of twins is only slightly less than that of the mother. Considering the grandchildren of twins he finds that the female of the pair produces 22.7 per cent. twin births whereas 21.7 per cent. of the births grandfathered by the male of the pair are twins. Clearly this is evidence that fathers have some causal relation to the production of multiple births.

*Is there inheritance of twinning tendency from the father's side? Verhandlungen des V Internationalen Kongresses fur Vererbungswissenschaft. Berlin, 1927.

Doctor Davenport believes that of the numerous double ovulations only one-fifth result in the production of twins, the others dying in the uterus, thus justifying the old German who, upon being congratulated on the birth of twins, remarked that "tousands and tousands of times you get noddings."

This interuterine death of so many zygotes is held to be due to lethal factors carried by the sperm which, if true, would account for the influence of the father in the production of twins. A strain characterized by a high percentage of multiple births is held to be one free from lethal factors and hence the males of such a strain (as well as the females) will engender a high percentage of twins. Whatever the merits of Doctor Davenport's explanation of the influence of fathers in twin production may be, his study of this group of two hundred families leaves little room for doubt that the expectation for twins among wives of men who are born as twins is very much higher than that for wives in general.

J. H. KEMPTON.

Books Received

BOOKS are acknowledged in this column as received, and such acknowledgment must be regarded as sufficient return for the courtesy of the sender. As far as space permits, books that contain material of special interest to the readers of the JOURNAL *will be reviewed in later numbers.*

HUMAN ASPECTS OF UNEMPLOYMENT AND RELIEF, *by* JAMES M. WILLIAMS. Pages 230 and XVI. The University of North Carolina Press, Chapel Hill, N. C. Price $2.50.

An intensely interesting and very moving book, but purely on an emotional plane as concerns any progress toward a permanent solution of our economic and social problems which so much need something more than palliatives.

THE BULPINGTON OF BLUP, *by* H. G. WELLS. 9 Chapters. 414 Pages. Price $2.50. Macmillan Co., New York, 1933.

"Adventure, poses, stresses, conflicts, and disasters in a contemporary brain."

GENETICS OF SHEEP, *by* E. WASSIN, B. POPOVA, Y. KARDEMOWICH, G. BAGOLUBOW and N. DIONYDOV. 165 Pages. 7 Chapters. Moscow, 1932.

Baa-baa black sheep, have you any genes?

GROWTH AND DEVELOPMENT OF THE CHILD, PART II: ANATOMY AND PHYSIOLOGY, A Publication of The White House Conference. 629 Pages. Price $4.00. The Century Co., New York, 1932.

THE FAMILY, A Study of Member Roles, *by* KATHARINE DUPRE LUMPKIN, Assistant Director, Council of Industrial Studies, Smith College. 180 Pages. 11 Chapters. Appendix. Price $2.00. The University of North Carolina Press, Chapel Hill, 1933.

SCIENCE AND CIVILIZATION, *by* GUY STANTON FORD. Twenty-nine Pages. The Day and Hour Series of the University of Minnesota, No. 1, 1933. Price 25 cents. The University of Minnesota Press, Minneapolis.

ZWILLINGSTUBERKULOSE, Zwillingsforschung und erbliche Tuberkulosedisposition, *by* KARL DIEHL and OTMAR FRHR. v. Verschuer, Kaiser Wilhelm Instuts fur Anthropologie. 500 Pages. 50 Illustrations. Bibliography. Index. Verlag von Gustav Fischer, Jena 1932.

TWO LIGULELESS GENES

Figure 12

Liguleless-2 is a newly discovered character in maize involving the loss of the membranous appendage at the junction of the blade and sheath of the leaf. It resembles closely a long known variation, liguleless-1, but is distinct from it as seen from the normal form of the leaves in the hybrid seedlings shown in the middle, which were produced by crossing the two Liguleless strains. Since ligules are *present* the distinction between the two genes is clearly demonstrated.

HERITABLE CHARACTERS IN MAIZE

XLVI—Liguleless-2*

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SINCE the liguleless condition in maize was first described by Emerson[2] twenty years ago, it has appeared on several occasions in strains presumably unrelated to Emerson's original Nebraska stock. The character is a simple recessive, and if it arose but once early in the history of the species it might have been carried down into many present day varieties from this common source. On the other hand, it is not unlikely that it has recurred from time to time as a mutation in normal maize. In either case it would be expected to come to light occasionally whenever two uniting germ cells both carrying the liguleless gene give rise to a seedling.

The first time the writer observed the liguleless character in maize outside of tester stocks being used for genetic studies, was in a single young plant in a farmer's field in Oxford County, Ontario. The variety being grown was a local strain of yellow dent. No opportunity was afforded of making any breeding tests with this individual.

In 1930 two progenies of the Golden Glow variety in the corn breeding plot on the University Hill Farms at Madison were found to be segregating for liguleless. One of these families was in the second selfed generation. The field records do not show that the parent line exhibited the character, but since the material was not scrutinized with anomalies of this sort in mind it may have been present. Possibly, however, it arose as a mutation at this time. Crosses were obtained between a few liguleless plants in the family and the standard liguleless stock familiar to maize geneticists. When the seedlings from this cross were grown in the greenhouse the following winter all were found to be liguleless. This stock, therefore, carried the same gene for liguleless as that already known.

The other strain of the Golden Glow variety segregating for liguleless was a once selfed family from a distinct stock, and was grown in the corn improvement plot in 1930 under progeny number 3118. The family consisted of about 40 plants approximately one-quarter of which showed the recessive leaf character. The hybrids between liguleless individuals in this progeny and the standard liguleless type all proved to have normal leaves. The liguleless condition in this progeny, therefore, was due to a gene hitherto unknown. It is proposed to call this new gene, liguleless-2 (lg_2), in contradistinction to the liguleless factor reported by Emerson, which may now be designated as lg_1.

In its main effects on plant structure lg_2 is very similar to lg_1. The distinctive feature of both is the absence of the ligule, a membranous appendage at the junction of the sheath and the blade of the leaf, and a marked reduction in the development of the auricle (See Figure 12). In addition to the features which Emerson[2] (1912 *a*) has described, lg_1 differs from normal maize in having a reduced number of branches in the tassel. It is interesting to note that lg_2 has a similar effect. In the original progeny segregating for the latter character the lg_2 plants, in striking contrast to their normal sibs, possessed but a single branch arising at the base of the long axis of the tassel. This extreme degree of suppression of branching of the tassel has not per-

* Papers from the Department of Genetics, Agricultural Experiment Station, University of Wisconsin, No. 148. Published with the approval of the Director of the Station.

sisted in lg_2 plants extracted from hybrids with various other stocks, however, although the tendency is still clearly evident. The original lg_2 plants were likewise about a week later in silking than their sibs but the expression of this feature also is dependent in considerable measure on the nature of the residual heredity.

The lg_2 gene lies in the A_1-Rg linkage group about midway between the a_1 and d_1 loci. Two progenies from selfed plants of the composition A_1lg_2. a_1Lg_2 gave 384 A_1Lg_2, 145 A_1lg_2, 140 a_1Lg_2 and 9 a_1lg_2 offspring. Such a distribution would result if a_1 and lg_2 are linked with about 27 per cent crossing over. The linkage is confirmed by the results of backcrosses of the double heterozygote in repulsion series to the double recessive as presented in Table I.* The four backcross progenies, containing 1011 plants in all, give a net value of 31 per cent crossing over between the two genes.

As may be seen from the results given in Table II,† lg_2 also shows linkage with d_1 (Emerson[3]), a gene known to lie in the A_1-Rg group at some distance from a_1 (Brink and Senn[1]). Three progenies from selfs of F_1 double heterozygotes in repulsion series were classified. With the aid of Immer's table[4] the amount of crossing over between lg_2 and d_1 is estimated to be about 33 per cent. From the known relations between the a_1 and d_1 loci it may be inferred that the order of the genes is $a_1 - lg_2 - d_1$. While a direct test has not yet been completed it seems probable that the position of the new gene lg_2 is in the vicinity of the nana (na) locus.

While the end effects of lg_1 and lg_2 are indistinguishable this does not necessarily mean that the genes are duplicate. The double heterozygote has typical leaves and tassel. The two respective recessive factors in homozygous condition may produce the same final phenotypic result by interrupting at different points the series of developmental events leading to the normal form.

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*TABLE $\frac{A_1 \quad lg_2}{a_1 \quad Lg_2} \times a_1lg_2$

Progeny Number	A_1 Lg_2	A_1 lg_2	a_1 Lg_2	a_1 lg_2	Total	Per cent. crossing over
W115	10	38	29	23	100	30.0
W116	61	108	122	32	363	34.6
W122	29	99	107	34	268	29.1
W123	37	102	93	40	278	28.3
Totals	104	347	351	149	1011	31.0

†TABLE $\frac{Lg_2 \quad d_1}{lg_2 \quad D_1} \times$ same

Progeny Number	D_1 Lg_2	D_1 lg_2	d_1 Lg_2	d_1 lg_2	Total	Per cent. crossing over
W109	212	105	82	15	414	36.2
W110	253	130	132	19	534	32.6
W111	145	69	63	6	283	28.2
Totals	610	304	279	40	1233	32.9

A Glossary Of Genetic Terms

GENETICS has developed so rapidly that many terms in common use in genetic literature are not yet incorporated in the dictionaries. Many people who are interested in heredity are bothered by such words, for which no definition can conveniently be found. For this reason, it is proposed to publish occasionally a glossary of terms which would not be readily understood and which are not to be found except in new unabridged dictionaries. It is realized that these definitions will probably not meet with universal approval and comments and suggestions will be welcomed.

ALLELOMORPH—Mendelian characters are inherited in alternative pairs, or in alternative series. These alternative genes are called allelomorphs. Examples: Albinism (recessive), Normal pigmentation (dominant); Horns (recessive), Hornlessness (dominant).

CHIASMA—"In the diptolene stage (of cell division) the chromatids are associated in pairs in such a way that in one part of their length two chromatids are associated but in another part each is associated with a different chromatid. The point of exchange is termed a chiasma." (Sansome and Phipp, 1932.)

"Exchange of partners between the four chromatids of a bivalent." (L. H. Hill, 1932.)

CHROMOSOMES—Tiny dark-staining bodies visible in the nucleus of the cell at the time of cell-division. The number of chromosomes in any species is usually constant. The chromosomes carry the genes, linearly arranged, which control the development of Mendelian characters.

DIPLOID—Having two sets of chromosomes. Body-tissues of higher plants and animals are ordinarily diploid in chromosome constitution.

DOMINANT—A character possessed by one of the parents of a hybrid, which appears in the hybrid to the exclusion of the contrasted character from the other parent (the recessive). Thus in a cross of green- and yellow-seeded peas the first generation has yellow seeds. Yellow is dominant and green is recessive, being transmitted but not appearing in the presence of the factor for yellow.

EPISTATIC—Non-allelomorphically dominant; i. e., "Dominance" refers to the interaction of two or more genes located at the same point on the chromosomes. Epistasy refers to dominance relations of two genes situated on different chromosomes.

FACTOR—Same as *Gene*.

F_1—(Pronounced eff-one). The first filial generation. The offspring of a given mating.

F_2—The second filial generation. Produced by intercrossing or self-fertilizing the F_1. The inbred grandchildren of a given mating.

GAMETE—A reproductive cell of either sex; e. g. sperm or ovum.

GENE—(1) The unit of inheritance, which is transmitted in the germ cells, and which by interaction with the genic and cytoplasmic complex controls the development of a character. The genes are arranged linearly in the chromosomes. (2) "The physical basis of heredity"—or more figuratively, the atom of the genetic molecule.

HAPLOID—Having the reduced number of chromosomes, as in germ cells, as distinguished from the diploid or double number of chromosomes in normal somatic cells.

HETEROZYGOUS—Containing both genes of an allelomorphic pair, or two genes of an allelomorphic series. Heterozygous individuals generally resemble the individuals homozygous for the dominant character, but they transmit the recessive to half their offspring.

HOMOZYGOUS—(1) An organism formed by like germ cells; (2) An organism is said to be homozygous for a given character when all the germ cells transmit identical genes for this character. This is the most frequently used meaning of the term.

HYPOSTATIC—Non-allelomorphically recessive. (See *Epistatic*.)

MULTIPLE SCLEROSIS—A disease in which patches of sclerosis (hardened tissue of chronic inflammatory origin) are scattered over the brain or spinal cord, or both. It is marked by peculiar jerky spasms of the arms, weakness of the muscles, incoordination, atrophy of the optic nerve, mental derangement, headache and vertigo, and staccato speech.

POLYPLOID—Normal body cells of the higher plants and animals have two sets of chromosomes (see DIPLOID.) Polyploids are forms having three or more of these basic chromosome sets.

RECESSIVE—See *Dominant*.

SEGREGATION—Separation of allelomorphic genes at meiosis.

SELFED—Self-pollinated.

TRIPLOID—An organism characterized by having three times the reduced primary chromosome number.

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